# The Stochastic Life-Cycle Model (SLCM): Simulating the Population Dynamics of Anadromous Salmonids

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RESEARCH SUMMARY

The Stochastic Life Cycle Model (SLCM) simulates the life cycle of anadromous salmonids and is designed to mimic the basic mechanisms regulating populations of Pacific salmon, while capturing some of the intra-annual and interannual variation inherent in these populations. This model was designed for population viability assessments combining advanced modeling techniques with concepts from the field of conservation biology.

While the basic structure of the SLCM is similar to other life-cycle models, it differs in several ways. First, the SLCM incorporates stochastic or probabilistic processes at each step in the life cycle. The binomial distribution is used extensively to introduce demographic stochasticity in survival; the beta distribution is used to introduce environmental stochasticity. Because of its stochastic nature, the model's predictions must be expressed in probabilistic terms. Multiple games are run using a Monte Carlo approach to generate probability distributions for future outcomes. Second, the model is designed to use inputs from more detailed models for specific life stages, in combination with a minimum number of empirically based parameters. SLCM users can choose among alternative models for the more contentious life stages, such as juvenile migration and adult harvest, incorporating the results of their preferred models. An ancillary calibration model has been developed that allows the SLCM to be fitted to a historical time trace of population estimates, constraining expectations of survival and their variances to historical levels.

The model also allows considerable flexibility in describing the dynamics of juvenile production. Users can choose among three density-dependent relationships to describe egg-to-smolt survival, including the Beverton-Holt, the Ricker, and a logistic response function, or use empirically based conditional probabilities. A variety of scenarios involving hatchery and natural production are possible, ranging from natural production only, to a combination of hatchery and natural production involving supplementation of adults, fry, or smolts. Allocation of naturally produced and hatchery-produced adults among terminal harvest and hatchery and natural spawning follows a set of adjustable rules that affords priority to natural escapement and hatchery broodstock needs.

The model is written in the SAS® programming language, which allows the model to operate on a variety of computing systems and provides enhanced flexibility in the analysis of model output. Users of the model need not be proficient in SAS. Simple input forms and ancillary programs to analyze model results allow users to run the model with a minimum of prior instruction.

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INTRODUCTION

Models are commonly used as exploratory tools to help fishery managers and planners estimate the potential effects of alternative harvest, mitigation, and enhancement strategies on target fish populations. Examples include Goodyear (1977), Taylor (1981), Walters (1981), Jensen and Hamilton (1982), Peterman (1982), and MacCall and others (1983). Within the Columbia River Basin, the Northwest Power Planning Council relies heavily on the System Planning Model (McConnaha 1992) for analysis of mitigation and enhancement opportunities for Pacific salmon and steelhead. Like many other models used in fisheries science, the System Planning Model is a deterministic model that is designed to mimic population dynamics. Within a deterministic model, simulated populations rigidly follow mathematical rules that govern survival through each life stage and from one generation to the next. Intrapopulation variability plays no role; interannual variation can be introduced only by changing annual inputs such as river flows.

The caricature of reality portrayed in a deterministic model is sufficient to guide management decisions in some cases, but can be dangerously misleading in others. To understand why, first consider their conceptual underpinnings. The more commonly used models of fish population dynamics were derived from surplus production models developed by fisheries scientists in the 1950's (Beverton and Holt 1957; Ricker 1954). These models were derived from the gross dynamics of major fish stocks observed over several years. The general response of these stocks to increased levels of fishing harvest led pioneering researchers to postulate simple models describing the population dynamics observed in the field. Paradoxically, these models have found wide acceptance among fisheries scientists despite the models' generally abysmal fit to empirical data (Rothschild 1986).

At best, deterministic surplus-production models capture only the central tendencies of a population. When combined with models that link management actions to model parameters, deterministic models can provide a normative ranking of alternative strategies if three conditions hold. First, the model must be valid for the population in question, that is, the model should faithfully mimic the population's underlying dynamics. Second, the population must be relatively robust so annual deviations from the expected behavior do not have long-term repercussions. And third, model parameters must be estimated accurately.

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In a sense, we can never be certain that these conditions hold true. We can be more confident with populous stocks where sufficient data provide a convincing argument for the model's use. Unfortunately, this is not the case for many stocks of concern, such as those within the Columbia River Basin and other coastal streams of the Pacific Northwest.

Addressing the uncertainty inherent in fisheries management requires us to restructure our perspective on planning and the use of models (Walters 1986). Some basic modifications in model design can help us cope with our inability to unerringly predict future outcomes. The first step toward a richer analysis that embraces uncertainty is to use stochastic models. Stochastic models can incorporate at least three sources of uncertainty: (1) temporal variation in population structure and environmental conditions, (2) intrapopulation variation among individuals, and (3) uncertainty in parameter estimates. All three sources of uncertainty can have important policy implications.

Nowhere is uncertainty in planning more critical than for stocks that have a high probability of becoming extinct or losing significant genetic resources through declining populations. Chance occurrences can be catastrophic for threatened or endangered species on the brink of extinction. Central tendencies or expected values are insufficient when dealing with these populations. The probabilities of catastrophic outcomes must be assessed using stochastic models that can simulate uncertainty. Deterministic models that consider only central tendencies have no place in the analysis of threatened or endangered species.

FUNDAMENTAL PRINCIPLES

Stochastic models are created in two basic ways. One option is to start with a deterministic model and recast the model parameters as random variables drawn from selected probability distributions. This option introduces little or no change in the basic model structure, but does require specifying probability distributions for each model parameter. Particular attention must be given to parameter estimation. The estimation procedure must explicitly include the proposed variance structure, and it should produce parameter estimates with meaningful statistical properties. For nonlinear models, the expected or mean values of model outputs such as population size will differ from the output of the deterministic model using mean parameter values. This result, which arises from Jensen's Inequality Theorem, illustrates the fallacy of assuming that the results of deterministic models using point estimates will be directly comparable to those of a properly constructed stochastic model, or that one can convert a deterministic model to a stochastic model simply by adding noise to the parameters.

The deterministic model with random parameters is not very satisfying conceptually because the deterministic relationships continue to be emphasized. Stochasticity in the model is essentially noise obscuring a deterministic signal. At the level of human resolution, however, nature is inherently stochastic, not deterministic. Therefore, it seems appropriate to build this inherent stochasticity into our models from the ground up.

A more proper way to incorporate nature's uncertainty is to use stochastic process models. In this approach, the focus is on the state variables in the model, rather than the parameters. Given the state of the system at time t, the likelihood or probability of all possible future states at time $t+1$ are assessed. The range of possible future states together with their

probabilities defines a probability distribution that is the fundamental building block of a stochastic process model.

A simple example can illustrate the differences among the different types of models. Consider the survival of a group of individuals from time t to $t+1$. Let $N(t)$ denote the number of individuals alive at time t, and $N(t+1)$ the number alive at time $t+1$. A simple deterministic relationship is

$$N(t+1) = N(t)p \tag{1}$$

where p = the proportion surviving through one time unit. If N is restricted to integer values, then similar restrictions must be placed on p as well. For example, if $N(t) = 10$, then $p = 0.5$ is reasonable. But if $N(t) = 9$, then p cannot be 0.5 because that will result in $N(t+1) = 4.5$ individuals, an unrealistic outcome. Simply rounding $N(t+1)$ to the nearest integer will not work. As long as $p \geq 0.5$, the population will never die out—as $t = 0,1,2, ...\infty$, $N(t) = 10,5,3,2,1,1,...,1$. In this model, the difference between $p = 0.5$ and $p = 0.4999$ is the difference between immortality and certain extinction.

This simple deterministic model could be made stochastic by defining a probability distribution for p. We would have to define at least one more parameter to describe the variance of p and also consider many of the same integer-counting problems that are associated with the deterministic model. While there are practical solutions for this simple, one-step example, the problems mount as more steps and more parameters are added.

The more elegant and parsimonious way to address this problem is to view it as a stochastic binomial process. In the binomial model, each individual is assumed to have the same probability of surviving (p). $N(t+1)$ is viewed as the sum of $N(t)$ independent trials with possible outcomes 0 or 1 (0 = individual dies, 1 = individual survives). This gives rise to the familiar binomial probability distribution

$$\text{Prob } \{N(t+1) = X\} = \frac{N(t)!}{[N(t)-X]!X!} p^X [1-p]^{[N(t)-X]} \tag{2}$$

which is defined for $0 \leq X \leq N(t)$ and has mean = $N(t)p$ and variance = $N(t)p[1-p]$. The binomial model is widely applicable as a model of death processes in ecology (Pielou 1977) and is used extensively within the SLCM. In the following discussion, the independent variables N and p used in the binomial distribution are assigned to a variety of state variables and probabilities, but their interpretation relative to the binomial distribution is the same.

Two extensions to the binomial, the multinomial and the binomial-beta distributions, are also used within the SLCM. The multinomial is appropriate when there are more than two possible outcomes, all outcomes are mutually exclusive, and all outcomes have fixed probabilities of occurring that sum to one. For example, the allocation of subbasin escapement among returns to the hatchery, subbasin harvest, natural spawning, and natural mortality follows a multinomial.

The binomial-beta distribution is used where the probability of survival (p) is not assumed to be constant, but rather is itself a random variable. The variation or uncertainty in p can result from three sources: (1) temporal changes in the environment or environmental stochasticity (Gilpin and Soulé 1986), (2) intrapopulation variability among individuals arising from

genotypic and phenotypic heterogeneity, or (3) uncertainty about the proper value of p resulting from experimental error. Press (1989) describes how the beta distribution arises as a model of uncertainty surrounding p in a binomial process, given limited information.

In the binomial-beta distribution, a beta distribution defines the probability distribution of p. Using the notation introduced above, the binomial-beta distribution is defined by

$$\text{Prob}\{N(t+1) = X\} = \frac{N(t)!}{[N(t)-X]!X!} \frac{\beta\{[X+a],[N(t)-X+b]\}}{\beta\{a,b\}} \tag{3}$$

where a and b are parameters of the beta distribution, and $\beta\{a,b\}$ is the beta function. The moments of the binomial-beta are

mean $= N(t)a / [a+b]$
variance $= N(t)ab[a+b+N(t)] / [(a+b)2(a+b+1)]$.

Boswell and others (1979) provide a fuller discussion of the derivation of the binomial-beta and its use in ecology.

While natural stochasticity and measurement error can be expressed in identical terms mathematically, they might have different implications when the results are interpreted. Thus, it may be useful to keep the two forms of uncertainty separate in an analysis. The SLCM has the capability to accommodate many such instances (see the operational notes below).

OVERVIEW OF MODEL

The SLCM can be thought of as a series of compartments corresponding to stages within the life cycle of anadromous salmonids. The total population is divided into two stocks, hatchery and natural. The natural stock includes all fish spawned in the wild and hatchery-produced juveniles that are released as fry, regardless of the origin of their parents (fig. 1). Similarly, the hatchery fish include all fish spawned in the hatchery and released as smolts (fig. 2). For much of their lives, hatchery-produced fish and naturally produced fish share a common life cycle. Transitions from one compartment to the next determine the model dynamics. At each transition, random draws from the appropriate probability distribution determine the values of the state variables (table 1). The model runs on an annual time step, but multiple transitions can occur within a single step. Each transition is described in more detail in the following sections. State variable names are given in capital letters and parameters in italics.

The model uses a set of production, passage, and harvest parameters (table 2) gleaned from the various input files (described below). A set of control parameters determines the number of replicates (games) within each simulation, and the number of years per game. The user must specify initial numbers for each life stage. As the model runs, it creates a data set containing identification variables and updates state variables at the end of each year. For simulation purposes, a "year" begins with natural spawning.

Currently, two versions of the base model are available, incorporating two different approaches to modeling production of juvenile migrants (smolts). Version 1 is more descriptive, as it tracks egg production and egg-to-smolt survival in a more conventional form. The user can choose among three different functional forms to describe density-dependence in early juvenile survival. Interactions between hatchery-released fry and
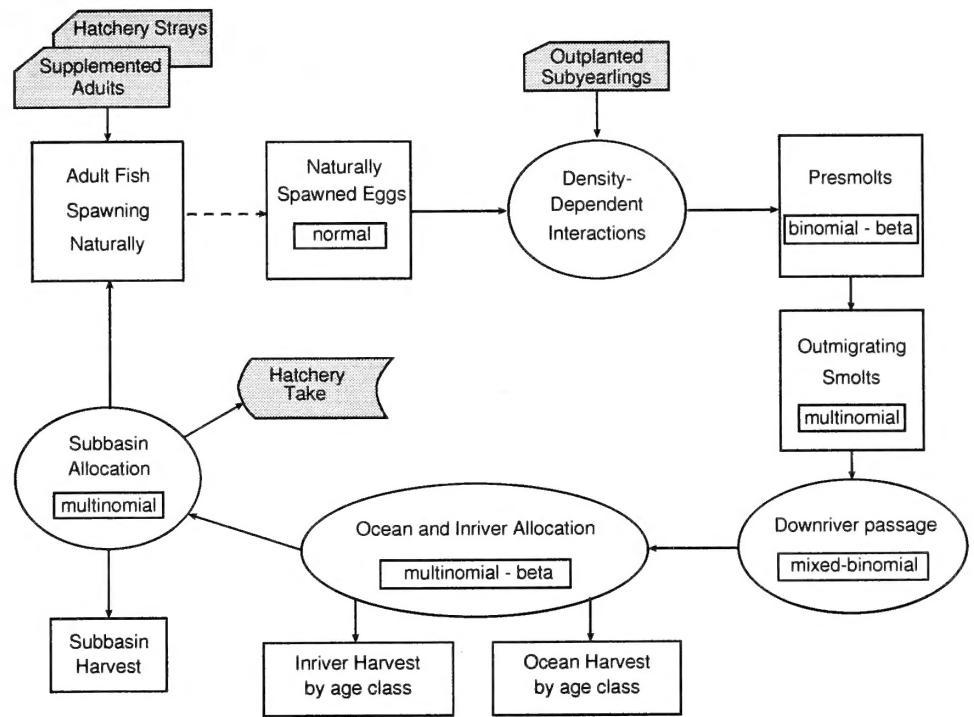
Figure 1—Flow diagram for naturally produced fish in the Stochastic Life-Cycle Model. Interior boxes denote probability distributions used in each step.
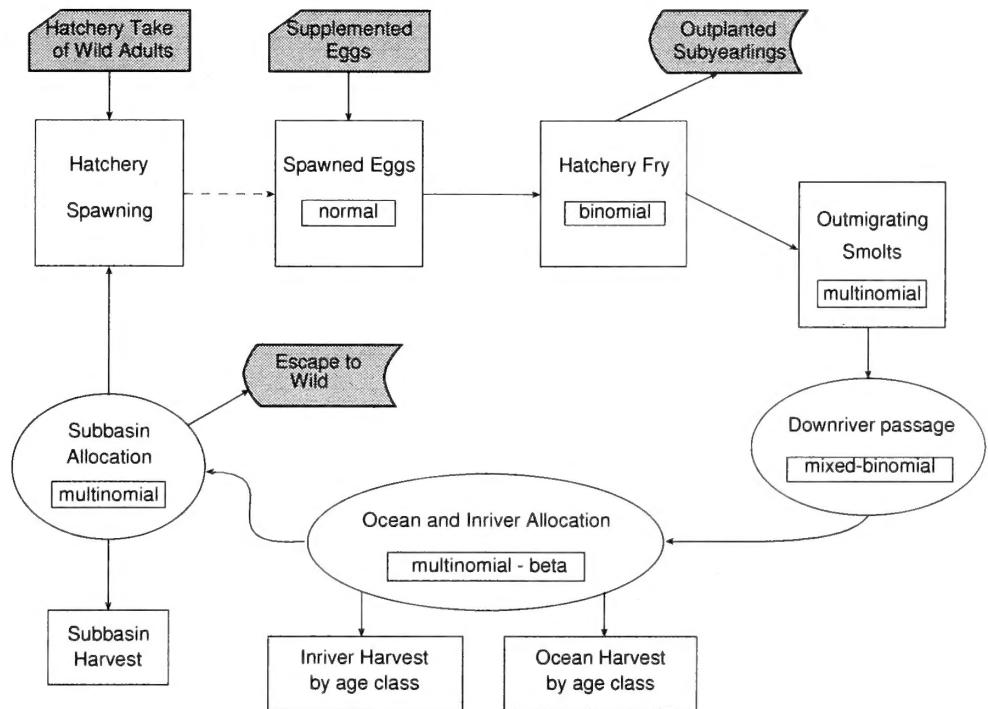
Figure 2—Flow diagram for hatchery-produced fish in the Stochastic Life-Cycle Model. Interior boxes denote probability distributions used in each step.

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Table 1—State variables used in the Stochastic Life-Cycle Model

Name	Description
Natural stock	
SPAWNERS	Spawning adults
FSPAWN	Female spawning adults
EGGS	Eggs spawned in the natural environment
PRESMOLT	Juvenile fish immediately before migration
SMOLT0	Subyearling juvenile migrants
SMOLTi	Juvenile migrants of age $i+$
SMT_BON	Smolts surviving to below Bonneville Dam
RECRUITS	Fish harvested in fisheries or escaping to subbasin
OiHARV	i-ocean fish harvested in ocean ($1 \leq i \leq 4$)
OiRVH	i-ocean fish harvested in Columbia River
OiSBE	i-ocean fish escaping to subbasin
OCHARV	Total ocean harvest
RVHARV	Total mainstem harvest
SUBESP	Total escapement to subbasin
SUBHARV	Subbasin harvest
TOTHARV	Total harvest
MAXHT	Number available to the hatchery
HATTAKE	Number taken by hatchery
Hatchery stock	
HSPAWNER	Spawning adults
HFSPAWN	Female spawning adults
HEGGS	Eggs spawned in the natural environment
HATFRY	Number of fry produced
FRYREL	Hatchery juveniles released as subyearlings
HSMOLT	Hatchery juveniles released as smolts
HSMT_BON	Smolts surviving to below Bonneville Dam
HRECRUIT	Fish harvested in fisheries or escaping to subbasin
HOiHARV	i-ocean fish harvested in ocean ($1 \leq i \leq 4$)
HOiRVH	i-ocean fish harvested in Columbia River
HOiSBE	i-ocean fish escaping to subbasin
HOCHARV	Total ocean harvest
HRVHARV	Total mainstem harvest
HSUBESP	Total escapement to subbasin
HSUBHARV	Subbasin harvest
HTOTHARV	Total harvest
HMAXHT	Number available to the hatchery
HSPAWN	Number taken by hatchery
ESPWILD	Number escaping to natural spawning areas

Table 2—Biological parameters and control variables used by the Stochastic Life-Cycle Model

Name	Description
Natural production parameters	
ffem	Probability of being female
prspsv	Prespawning survival probability
egfem	Mean eggs per female
stdegg	Standard error of mean eggs per female
jackspn	Spawning contribution of one-ocean fish (0-1)
logtscl	Logistic response scale parameter
alpha	Density-independent juvenile production parameter
beta	Density-dependent juvenile-production parameter
cvegsv	CV of egg-to-presmolt survival
stayi	Conditional probability of staying over ith winter
inbsmsv	Subbasin presmolt-to-smolt survival
basercv	Fraction recovered as adults in calibration years
cvadtrv	CV of *basercv*
minesp	Minimum escapement goal
maxthar	Maximum terminal harvest (number)
Hatchery stock parameters	
hffem	Probability of being female
hprspsv	Prespawning survival
hegfem	Mean eggs per female
hstdegg	Standard error of mean eggs per female
egg_fry	Egg-to-fry survival rate
hfry_sv	Initial subyearling survival following release
fry_smt	Fry-to-smolt survival rate
hsmt_sv	Initial yearling survival following release
hjackspn	Spawning contribution of one-ocean fish
hbaserv	Fraction recovered as adults in calibration years
hcvadtrv	CV of *hbaserv*
hstray	Conditional contribution to wild escapement
htermhar	Terminal harvest rate
Hatchery management parameters	
adtsup	Additional adult supplementation to wild
colrate	Hatchery collection efficiency for natural fish
hcolrate	Collection efficiency for hatchery fish
minrun	Minimum natural escapement before hatchery take
hatrem	Target take of natural fish by hatchery
hatneed	Total adults needed by hatchery
htarget	Minimum acceptable level of egg capacity
eggcap	Hatchery egg capacity
fryplant	Fraction of fry released as subyearlings
fryint	Level of interaction between natural and released hatchery subyearlings (0-100)
Adult recovery parameters	
(h)ocnihar	Fraction of i-ocean fish harvested in ocean ($1 \leq i \leq 4$)
(h)ocnirvh	Fraction of i-ocean fish harvested in mainstem river
(h)ocnisuv	Fraction of i-ocean fish reaching next age class
(h)ocnisbe	Fraction of i-ocean fish escaping to subbasin
Passage parameters	
(h)msurv	Mean juvenile passage survival rate
(h)passcv	CV of juvenile passage
Control variables	
ngames	Number of games per simulation
years	Number of years per game
smttog	Selects juvenile production function
	1 = logistic response
	2 = Beverton-Holt
	3 = Ricker
	4 = empirical model (other parameters apply)

natural fry can be incorporated. Alternatively, Version 2 describes the steps between spawning and smolt production less explicitly, relying on historical information on adult production to generate smolt numbers. Each version is described in more detail below.

The following description applies to the base model. Specific changes in model structure have been made in various versions to accommodate special circumstances or life history traits peculiar to individual stocks, or to simulate specific hatchery scenarios. Such changes are easily made.

Natural Production of Juveniles: Version 1

The number of female spawners (FSPAWN) determines the number of naturally produced eggs. The number of female spawners is assumed to be binomially distributed with N = the number of spawning adults, and p = *ffem*, the probability of being female. The number of eggs is then simulated as a random normal deviate with mean = FSPAWN•*egfem* and standard deviation = FSPAWN•*stdegg*, rounded to the nearest positive integer. Since the number of eggs produced is the sum of reasonably large numbers of independent random variates (individual spawnings), the normal approximation seems justified.

The SLCM's only density-dependent mechanisms are in the egg-to-presmolt transition. Density-dependent mechanisms operating within the first year or two of life are assumed to play an important role in the dynamics of salmonid populations. The expected probability of survival from the egg stage to just before leaving the subbasin (PRESMOLT) is calculated as a decreasing function of initial egg numbers and hatchery fry releases (details below).

Numerous studies of the relationship between population density and survival indicate that the relationships—when detectable at all—are rather imprecise (Peterman 1987; Rothschild 1986). In addition, factors other than population density can contribute to large variations in early freshwater survival (Alderdice and others 1977; Kocik and Taylor 1987; Randall and others 1987). For this reason, the SLCM uses a binomial-beta distribution to generate the number of presmolts produced each year. The binomial-beta distribution increases the variance in the number of presmolts produced from a given number of eggs beyond that introduced by the binomial process alone. The coefficient of variation in egg-to-presmolt survival (*cvegsv*) is specified by the user as part of the input parameters. The model uses the expected probability of survival calculated from the density-dependent relationship and *cvegsv* to calculate the parameters of the beta distribution used in this transition.

The user can choose among three options for the density-dependent relationship used to calculate the expected egg-to-presmolt survival. The choices include the Beverton-Holt relationship (Beverton and Holt 1957),

$$E(p) = \frac{alpha}{\left[1 + \frac{(alpha\text{Eggs})}{beta}\right]} \tag{4}$$

the Ricker relationship (Ricker 1954),

$$E(p) = alpha[e^{(-beta\text{EGGS})}] \tag{5}$$

or the logistic response function,

$$E(p) = logitscl \ \frac{e^{(alpha+betaEGGS)}}{1 + e^{(alpha+betaEGGS)}}$$ (6)

The advantage of the logistic function is that it allows greater flexibility in defining the shape of the relationship between egg density and survival (fig. 3). With the Beverton-Holt and Ricker models, the greatest decline in survival always occurs at the lowest densities. With the logistic function, we can establish threshold levels where the density-dependent effects are most acute and survival decreases most rapidly. Note that the logistic model produces a dome-shaped egg-to-presmolt relationship similar to the Ricker model.
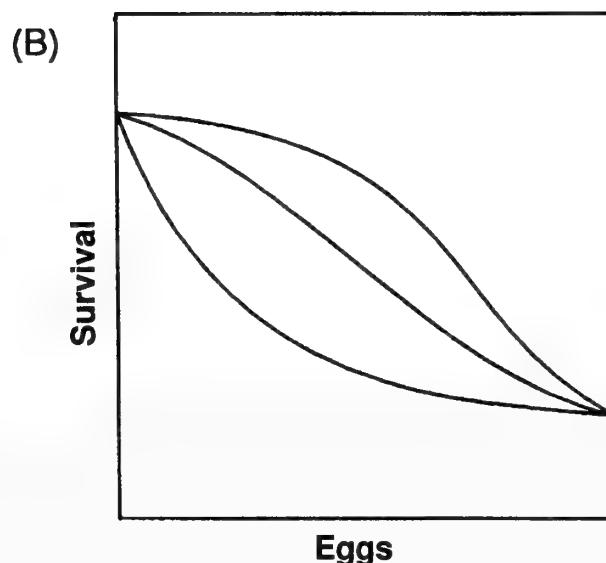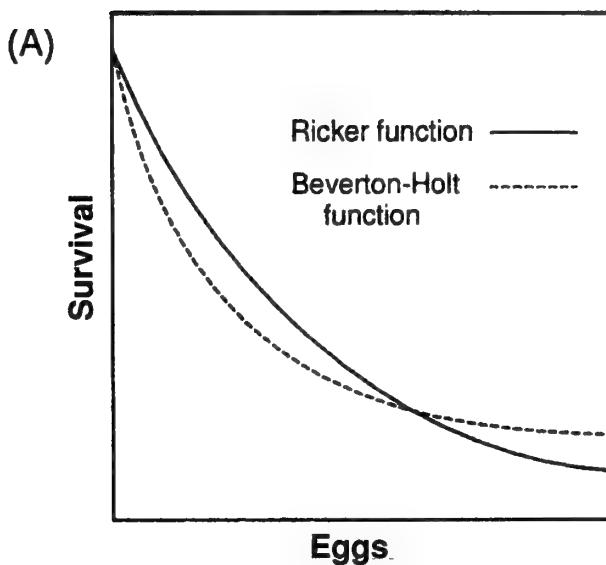
Figure 3—General shape of the relationship between initial egg density and egg-to-smolt survival generated using the Beverton-Holt and Ricker models (A) and various parameter combinations with the logistic response function (B).

The SLCM includes the option of integrating hatchery-released fry or subyearlings into the simulated natural populations. In the base model, the number of fry released by the hatchery (FRYREL) is first adjusted for post release mortality using the survival parameter, *hfry_sv*. The surviving fry interact with the natural fry according to the parameter, *fryint*. This parameter expresses interaction on an arbitrary scale that ranges from 0 to 100. If *fryint* = 0, then hatchery fry have no effect on survival of natural fry; if *fryint* = 100, hatchery fry affect the survival of natural fry to the same extent as additional natural fry. Expected survival of naturally spawned fish and hatchery-released fish is calculated in a multistep process outlined in appendix A. Admittedly, this process is arbitrary and rather convoluted. The method has two desired properties: (1) survival of naturally spawned fish decreases when hatchery-released fish are present and (2) the impact of hatchery releases on naturally produced fish is directly proportional to the degree of competition.

The base SLCM accommodates up to four year-classes of migrants. Subyearling migrants (SMOLT0) exit the tributary during the same year they are spawned; yearling and later migrants (SMOLT1 – SMOLT3) exit in succeeding years. Each additional year that the presmolts remain in the tributary they are subject to a mortality factor reflected in *inbsmsv*.

Alternative Model of Juvenile Production (Version 2)

In many instances, we do not have the stock-recruitment information needed to unambiguously choose one form of the juvenile production function over other alternatives. Available data may be scarce, providing no hint of the underlying relationship, or the data may be so noisy that no single function provides a superior fit. Where few or no data are available, little can be done to inspire confidence in the quantitative output of any model. Information from similar stocks might help, but in the end the chosen relationship must be viewed as a hypothesis entailing considerable uncertainty.

In instances where data are available but the underlying relationship is obscured, an empirical approach based on conditional probabilities may be used. This offers a way to capture the variation in recruitment, and to some extent, the density-dependent relationships that might exist. Data on spawning stock size and the estimated number of smolts produced from each spawning are compiled. Lognormal distributions are independently fit to the spawning and smolt production data; these are known as the marginal distributions. Smolts produced is plotted against spawning escapement in a two-dimensional graph. Reference lines are drawn to separate the marginal distributions into thirds, thus dividing the plot into nine cells (fig. 4). Dividing the number of points in a given cell by the sum of the three cells in its column provides an estimate of the conditional probability that the number of smolts produced in a given year will fall within that region of the graph, given that the corresponding spawning escapement is within the indicated range. These probabilities, along with the parameters defining the marginal distributions, must be specified in the SLCM parameter file if this option is used.

The SLCM uses these probabilities in a three-step process. First, it takes the number of spawners and determines which third of the spawning distribution is represented. Then, using the conditional probabilities, it randomly selects from a multinomial distribution the region of the smolt distribution that will be used to generate the number of smolts produced.
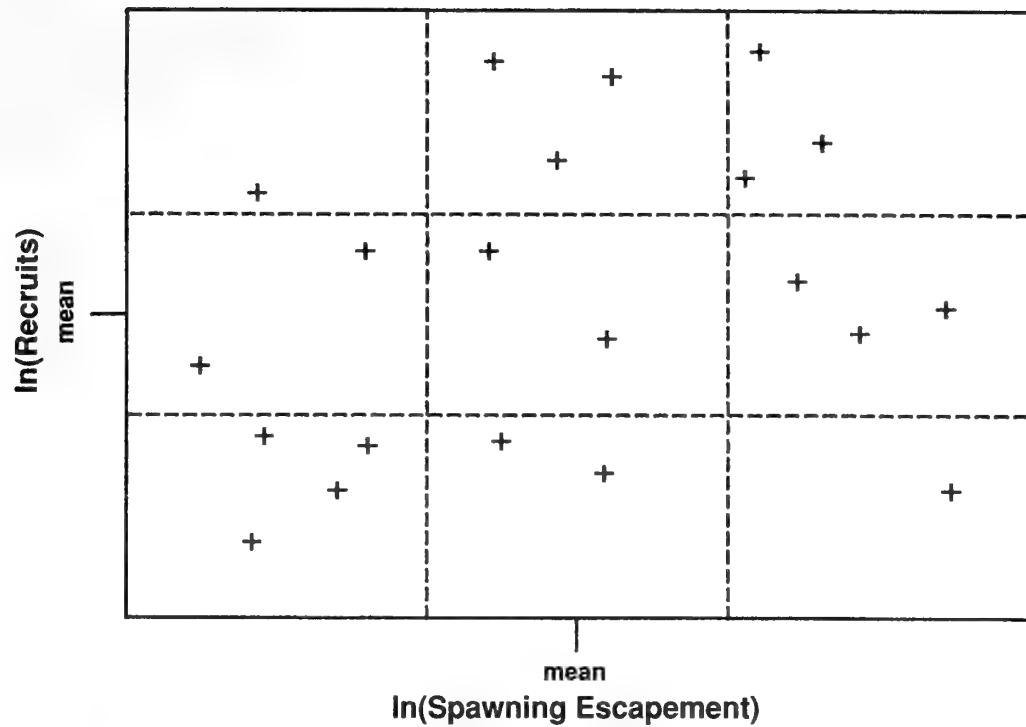
Figure 4—Natural logs of stock-recruitment data plotted in two dimensions. Dashed lines separate marginal distributions of stock and recruits into equal thirds, allowing computation of conditional probabilities.

Finally, it randomly selects a smolt production level from within the selected region of the marginal, lognormal distribution of smolts.

The SLCM does not allow for density-dependent interactions between natural fry and hatchery-released fry when Version 2 is used.

Hatchery Production

The number of eggs produced in the hatchery (HEGGS) is a random variate drawn from a normal distribution, where the mean and variance of the distribution are a function of the number of females spawned in the hatchery and the specified fecundity parameters. If hatchery egg production does not meet the minimum level defined by *htarget •eggcap*, then additional eggs (from an external source) are added to the hatchery stock. The number of fry produced is a binomial random variate with N = HEGGS, and p = *egg_fry*. The fraction indicated by *fryplant* is released as sub-yearlings; those remaining are released as yearling smolts the following year. The parameters, *fry_smt* and *hsmt_sv*, determine the survival from fry to yearling smolts within the hatchery and the initial survival of smolts shortly following release.

Juvenile Passage

The migration of smolts from upstream rearing areas to the estuary can be a critical period for many stocks. It is especially acute for those that make extensive migrations. For upper Columbia and Snake River populations, the migration path may include up to nine mainstem hydroelectric dams and associated reservoirs. Thus, there are good reasons for having a separate component for the juvenile migration period (juvenile passage).

Juvenile passage is expressed in the SLCM as a binomial-beta process. The number of smolts surviving downstream migration is a binomial random variate, where the survival probability (p) is drawn from a beta distribution. The expectation and variance of p can be estimated using auxiliary passage models that address this stage of the life cycle in more detail. In our analyses of Columbia Basin stocks, we used CRiSP, a passage model developed at the University of Washington, to estimate survival from tributary rearing areas to the Columbia River Estuary. (Information on CRiSP can be obtained from James Anderson, Center for Quantitative Sciences, University of Washington, Seattle, WA.) The parameters of the beta distribution were estimated from a set of survival estimates based on randomly generated flow conditions. In earlier analyses, we used a fourth-order autoregressive model with a random normal error term that was fit to CRiSP output. Results from both approaches were similar. Other passage models can easily be substituted for CRiSP.

Ocean and In-river Allocation of Adults

The advent of the coded wire tag (CWT) has permitted large-scale mark and recapture experiments on Pacific salmon from the Columbia River Basin. Of the millions of tagged fish released each year, however, only a small fraction of the tags are recovered. These recoveries provide a large bank of information on the age-specific relative distribution of recaptured adults among the several recapture sites, including ocean fisheries, in-river fisheries, and hatchery racks or other in-basin recovery sites. Unfortunately, the tag recovery data will never be sufficient to establish the absolute, age-specific probabilities of dying in the ocean, returning to the river, being harvested in the ocean or river, or dying in the river—parameters often included in management models. These population parameters can never be known precisely because there are more unknown parameters than recovery sites. Fish that die of natural causes are never seen. Thus, one cannot be sure if they died early or late in life. The best that CWT data can suggest is the magnitude of the total mortality loss—that proportion of the population that is never recovered or otherwise accounted for.

Rather than modeling age-specific mortality rates and maturity schedules, the SLCM is set up to correspond to the empirical model suggested by CWT recovery data. The total number of adults recovered is simulated using a binomial-beta distribution. Again, the beta distribution is used to introduce added stochasticity. A multinomial process is used to allocate the total number of fish recovered by age class among ocean harvest, in-river harvest, and return to the subbasin. Appendix B shows how the model calculates adult recovery parameters from CWT data.

Other models that simulate ocean and in-river harvest, such as a model developed by the Oregon Department of Fish and Wildlife (1991), can be used to estimate ocean and in-river recovery probabilities. In such cases, the simulated harvest and escapement data are used instead of CWT data. Harvest patterns that change with time are accommodated by using a special subroutine that calculates cohort-specific recovery probabilities using simulation results from the harvest model. Since the total fraction recovered depends on harvest and mortality rates, *adtrecv* is adjusted for each cohort to reflect changing conditions.

Subbasin Allocation

Allocation of adults returning to the subbasin follows a multinomial process, with the twist that hatchery needs and natural escapement targets have priority over harvest. Hatchery and natural adults are allocated among hatchery spawning, natural spawning, and terminal harvest according to a suite of parameters that direct the allocation process shown in figure 5. The number of fish available to the hatchery is determined by the
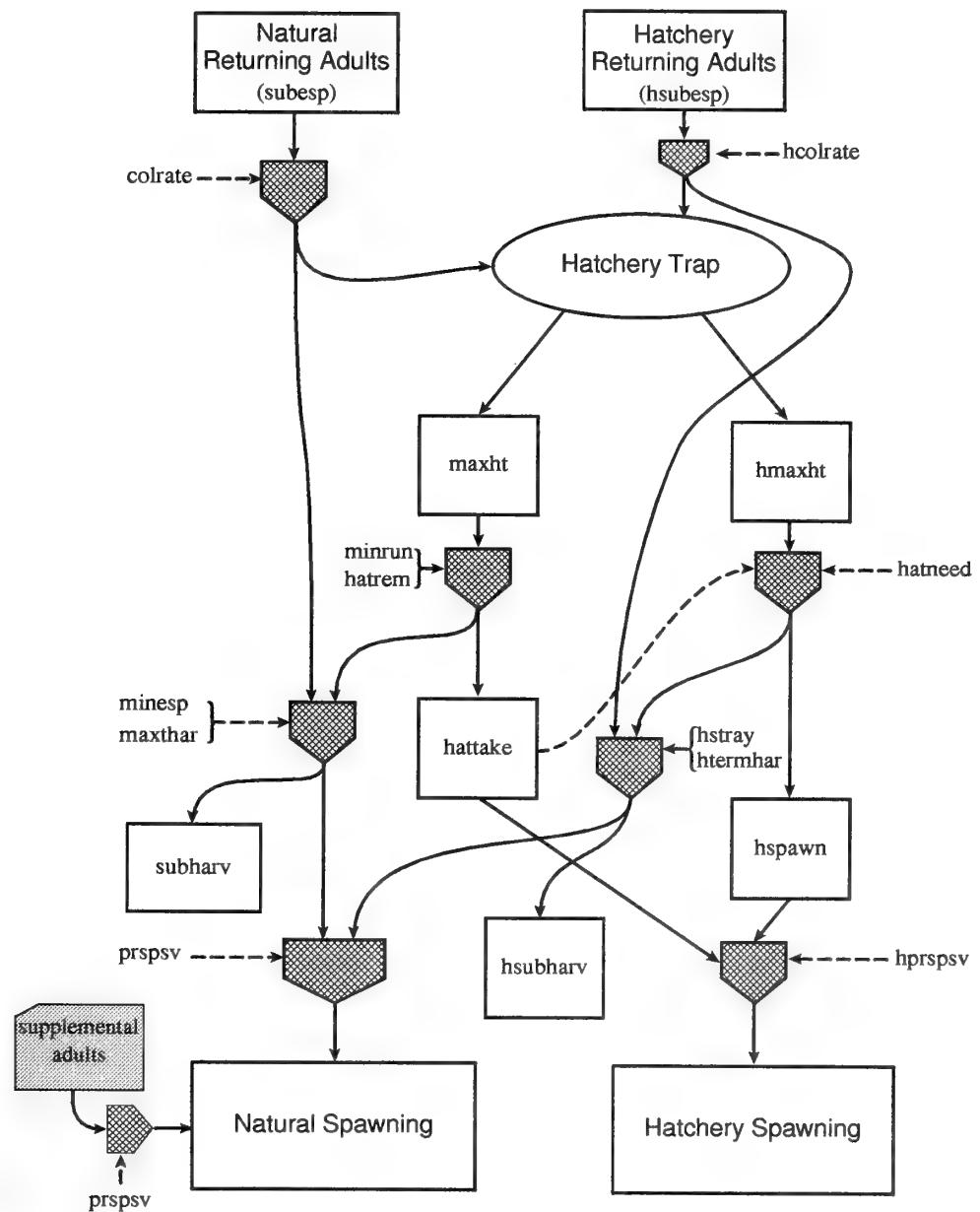
Figure 5—Conceptual flow diagram of hatchery take and natural escapement of adults. The abbreviations are explained in table 1.

hatchery trap efficiency, which can be different for natural and hatchery fish. Of the natural fish that are available, the hatchery removes the smaller of *hatrem* (the hatchery target) or those available in excess of *minrun* (the minimum acceptable wild escapement). The remainder of hatchery needs are met using returning hatchery adults, if available. Adults not needed by the hatchery and those escaping the trap are subject to a terminal harvest, with independent rates for hatchery and natural fish. Hatchery adults which escape harvest stray into natural spawning areas in proportion to the parameter, *hstray*. (This parameter may also incorporate the differential spawning success between natural and hatchery fish in the wild.) The total number of adults spawning naturally includes both natural and hatchery adults, and an additional number of adults, *adtsup*, which originate from outside the system (simulating adult supplementation). All adults are subject to prespawning mortality, either within the hatchery or natural areas. Jacks (one-ocean fish) can be excluded from the spawning population by using the parameters, *jackspn* and *hjackspn*.

Operational Notes   The SLCM and ancillary programs are written in the SAS programming language. While the model has been developed on a SUN workstation, it can be transferred easily to any system equipped to run the SAS language. Copies of files needed to run the model and produce summary analyses are available from the authors. The modular code can be modified to suit the particular needs of various user groups.

Once the SLCM files are installed, users run the model by setting up three parameter files, a file containing initial numbers, and a control file. Examples are shown in appendix C. These files can be modified by using a convenient text editor. Only the control file needs to be submitted as an SAS program. If the control file is set up properly, it will make all necessary calls to other files and programs. As output, the model creates an SAS data set containing all variables requested in the control file. Model results can be analyzed using ancillary SAS programs supplied with the model. Users may write additional ancillary programs to meet their specific needs.

The control file includes macros that allow users to perform multiple runs of the model using stepped parameters (each run would consist of multiple games), and to change parameters for specific years within games. This is useful in performing sensitivity analyses and in simulating environmental changes over time. The stochastic properties of the model can be changed through this mechanism by introducing additional uncertainty or changing the distributional properties of the parameters.

The control file also contains an SAS macro variable, &HATCHERY. Setting &HATCHERY to "off" shuts down all hatchery production. The simulated population then will contain only naturally produced fish.

ILLUSTRATIVE MODEL RESULTS

We demonstrate the SLCM using parameter sets listed in appendix C. These parameters were chosen to reflect a stock that is not limited by habitat, but by a low smolt-to-adult survival rate. Thus, the density-dependent parameter (*beta*) is set at a very low level. In this example, subbasin escapement (natural and hatchery) is the principal output examined. Our base case is a contrived fall chinook example that is not meant to mimic

any particular stock. The base case includes an assumption of little interaction between hatchery and natural fish, small amounts of fry releases (the bulk of hatchery releases are smolts), and no adult supplementation. Almost all surplus hatchery fish are harvested. The logistic response function is used to describe juvenile production.

Single Game

The simulation of a single population over a 500-year period is shown in figure 6. The population's fluctuation over time is typical of the fluctuations of state variables within the SLCM. Though we have not rigorously compared the model output with empirical time series, the results appear consistent with general observations of populations in nature.

A second way of viewing simulation results is to look at the relationship between the number of adults spawning naturally in a given year and their offspring recovered in future years as adults. In figure 7, SPAWNERS and associated RECRUITS for the 500-year period are plotted along with deterministic representations of the underlying spawner-recruit relationship. The curved line represents the density-dependent relationship between the number of spawning adults and the expected number of recruits. The straight line is the inverse of the relationship between a given number of recruits and the number of spawners they would produce. In a deterministic model, the population would move quickly to the equilibrium point determined by the intersection of the two lines.

In contrast, the SLCM suggests no single equilibrium point, but rather a broad clustering of points located near the deterministic equilibrium points. The first moment of the mass of point scattered within the spawner-recruit plane is actually located below and to the left of the intersection point. This suggests that while stochastic processes in the SLCM occasionally lead to production levels much higher than average, average production is less than predicted by deterministic models.
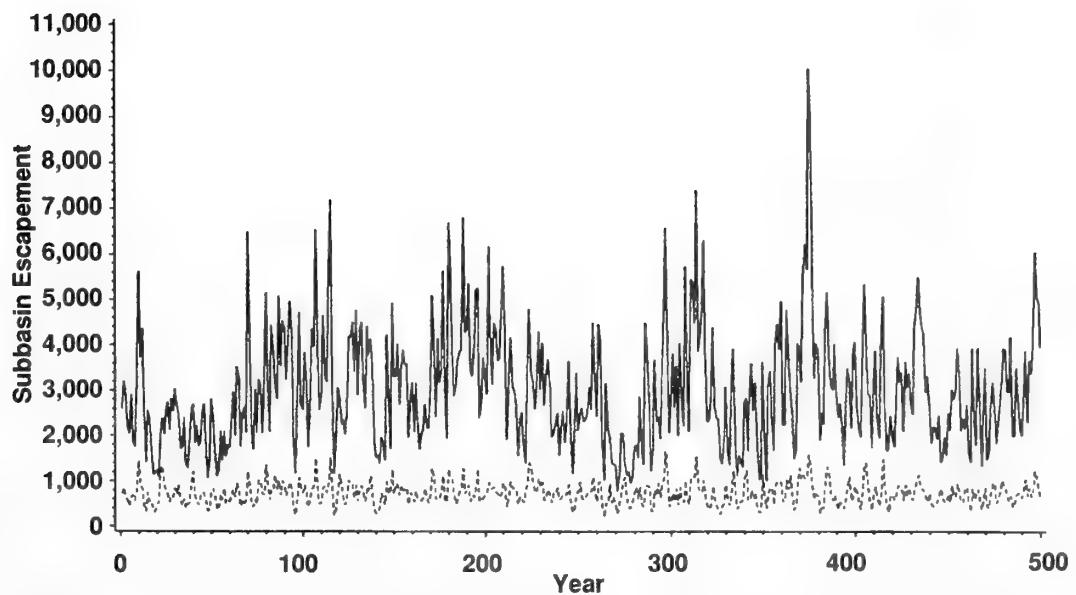
Figure 6—Subbasin escapement for a single simulation over time. Solid line indicates natural fish, dashed line indicates hatchery fish.

15
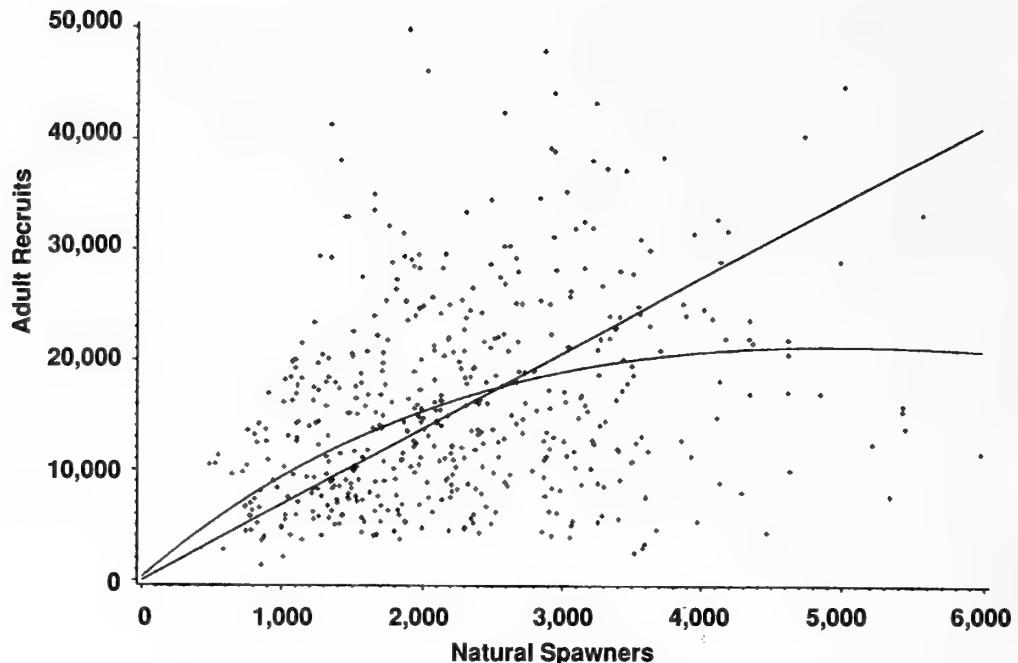
Figure 7—Simulated data showing the number of adult recruits produced by a given number of spawning adult salmon. The curved line represents the density-dependent relationship between the number of spawning adults and the expected number of recruits. The straight line is the inverse of the relationship between a given number of recruits and the number of spawners they would produce.

Multiple Games

Since the stochastic nature of the SLCM produces a different outcome for every game or simulation, the outcome from a single game is of little value. It is more informative to run multiple games and examine the output collectively. In this manner, one can evaluate possible future states probabilistically. For example, we ran 500 games covering 50 years each using the SLCM. When combined, the output from these games creates a probability distribution for each year, such as the distribution of spawners in year 50 (fig. 8). The distribution shown in figure 8 is characteristic of the positively skewed distributions of state variables common to SLCM results.

Portraying the distribution of a state variable through time is problematic. In figure 9, contour lines show the shape of the distribution of spawners through the simulation period. The contour lines depict the minimum, 10th percentile, median, mean, 90th percentile, and maximum from the 500 games. For this example, the bulk of the distribution is fairly stable, with the most variation occurring in the upper tail of the distribution.
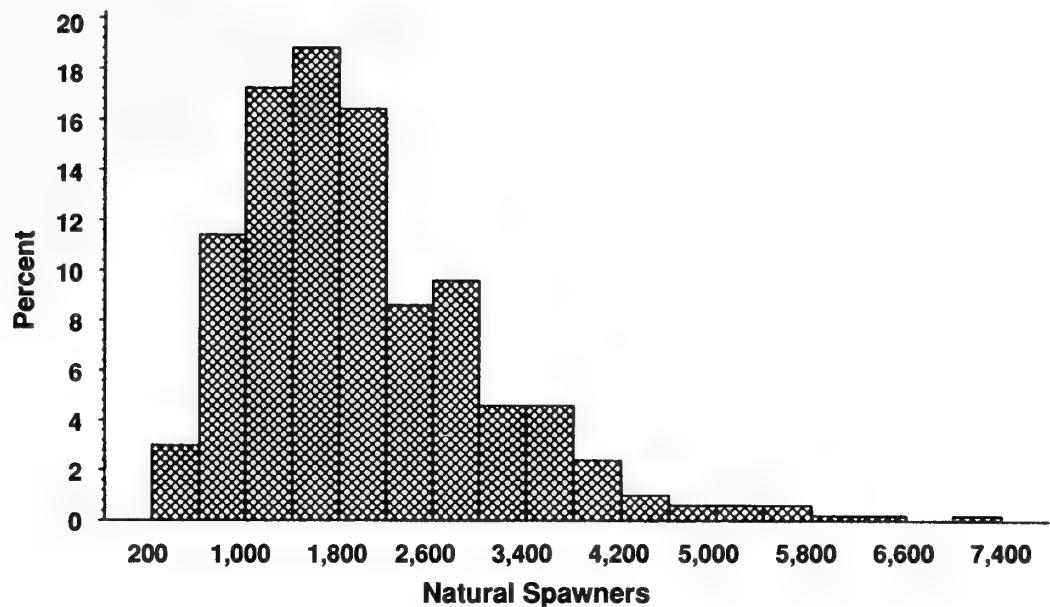
Figure 8—Distribution of the number of natural spawners in year 50 from 500 simulations.
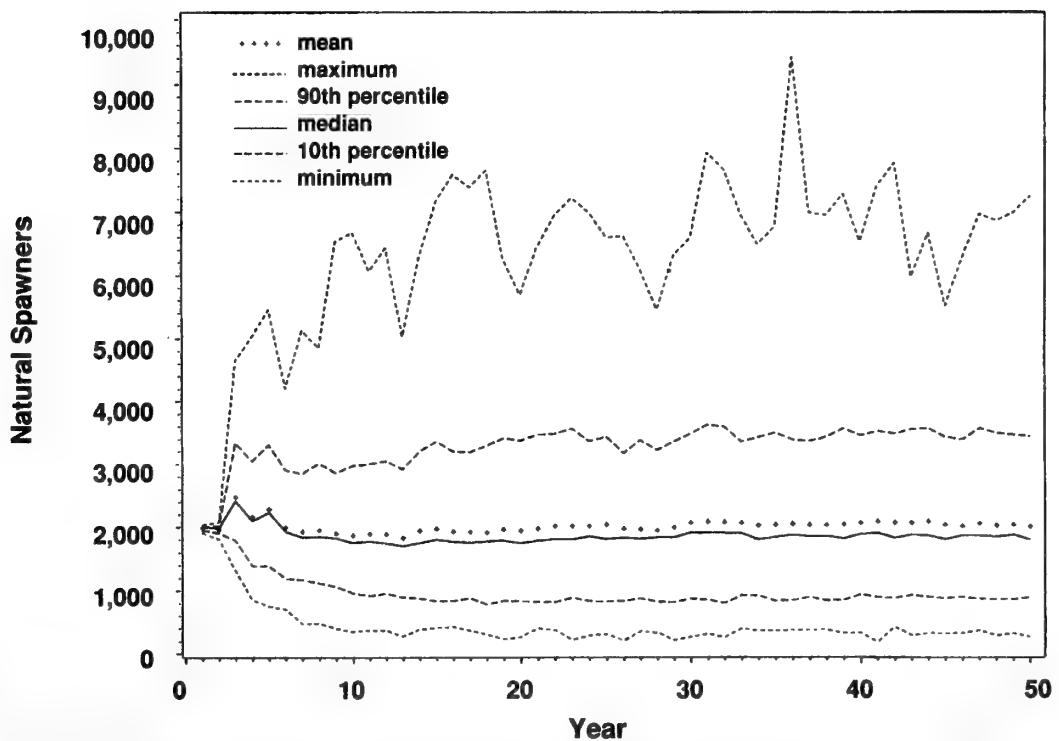
Figure 9—Distribution of natural spawners over time from 500 simulations.

Paired Comparisons

Models are often used to examine the relative effectiveness of alternative management proposals for increasing fish production. The effects of management changes could be lost or confounded with random fluctuations introduced by stochastic models such as the SLCM. To facilitate meaningful comparisons of alternative management proposals, the SLCM is designed to allow the user to control the random number streams used within the model. This allows users to replicate serial patterns within the SLCM reflecting changes in environmental conditions over time. Thus, a user could compare two or more management alternatives over the same temporal patterns in survival. For example, figure 10 shows two time series for a matched pair of games where downstream migrant survival has been increased by 40 percent in the second game. While there is independent variation in each game, a significant portion of the variation is shared. Multiple paired comparisons can lead to distributions of comparison statistics in much the same way that multiple games lead to distributions of state variables.

SENSITIVITY ANALYSIS

The structure of the SLCM allows explicit inclusion of parameter uncertainty in the model. By increasing the variance of survival processes, users can include some of the existing uncertainty about survival or production parameters. But increasing the variance only addresses questions of precision; it does not directly address problems of accuracy that arise if the parameter estimates are biased. A rigorous sensitivity analysis is needed to assess the ramifications of potential bias in parameter estimates.

The SLCM's relatively straightforward structure allows sensitivity analyses to be performed easily. The model can be reduced to five major components: density-independent juvenile production and survival,
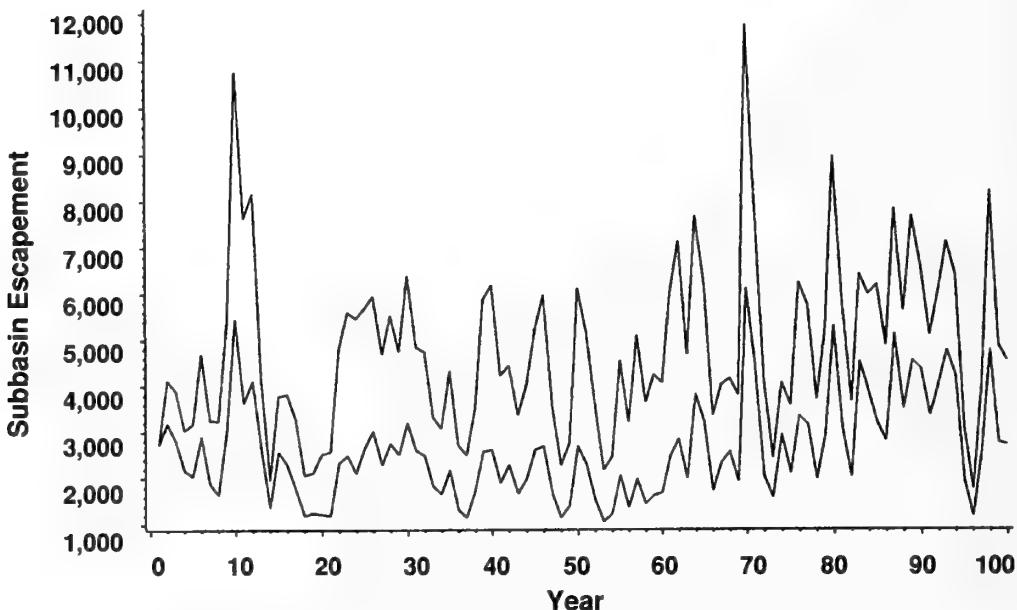
Figure 10—Paired comparison of model results using two levels of passage survival: 32 percent (lower line) and 44.8 percent (upper line).

density-dependent juvenile survival, downstream passage, adult recruitment, and harvest. The expected system response in each component can be reduced to a linear combination of certain model parameters (or a single parameter in some cases). Thus, users can select a small subset of parameters to serve as surrogates for all parameters when conducting a sensitivity analysis.

In a preliminary sensitivity analysis, we examined the sensitivity of the natural population to parameter changes by systematically varying *logitscl* and *adtrecv* to reflect different levels of early juvenile and postsmolt survival, varying *mpass* to reflect changes in downstream migrant survival (passage survival), and varying the fraction of recruits within a given age class that escapes to the subbasin (as opposed to being harvested). These four factors were varied in combinations to create two-dimensional matrices of parameter sets (either 11 x 11 or 10 x 10, depending on the variables). Within each matrix, *logitscl, mpass,* and *adtrecv* varied by a factor of three, while the proportion of nonharvested fish varied by a factor of ten (0.1 to 1). Five hundred games were simulated for each parameter set. Number of spawners in years 15 and 100 were compared across all parameter combinations. The number of spawners in year 15 proved to be a good indicator of short-term stock dynamics, while the 100-year results were better indicators of long-term effects.

Results of the Sensitivity Analysis

Some comments on the sensitivity of the SLCM to changes in parameters are appropriate, though we refrain from a detailed discussion. First, the distribution in number of spawners is very sensitive to changes in parameter values of the magnitude that we examined. Most sensitive is the upper tail of the distribution, which changes rapidly following parameter changes.

Second, short-term model results are more sensitive to changes in adult survival than to changes in juvenile survival. The mean number of spawners in year 15 was greater following increases in adult survival than after equivalent increases in juvenile survival. This is understandable because of the time lag required before changes in juvenile survival manifest themselves in changes in spawning escapement. Given a longer time period (such as 100 years), equivalent changes in juvenile survival and adult survival produced equivalent effects. However, the management implications of the apparent short-term effectiveness of increasing adult survival should not be ignored.

Among the variables that we examined, the model first appeared to be most sensitive to changes in passage survival. On further inspection, the apparent sensitivity to passage survival could be explained by the relatively low variance used for passage survival compared to the variance used for juvenile and postsmolt survival. The SLCM, like other stochastic models of this type, is most sensitive to the survival factor with the lowest variance. The interplay between survival and variance in survival can be demonstrated by plotting the changes in the mean number of spawners as the coefficient of variation (CV) in egg-to-adult survival increases (fig. 11). While the decline in the mean number of spawners is significant, the increase in the CV of state variables such as the number of spawners is more dramatic. We observed that the relationship between the CV of spawners and the CV of survival had a slope that is very close to (but slightly greater than) one.
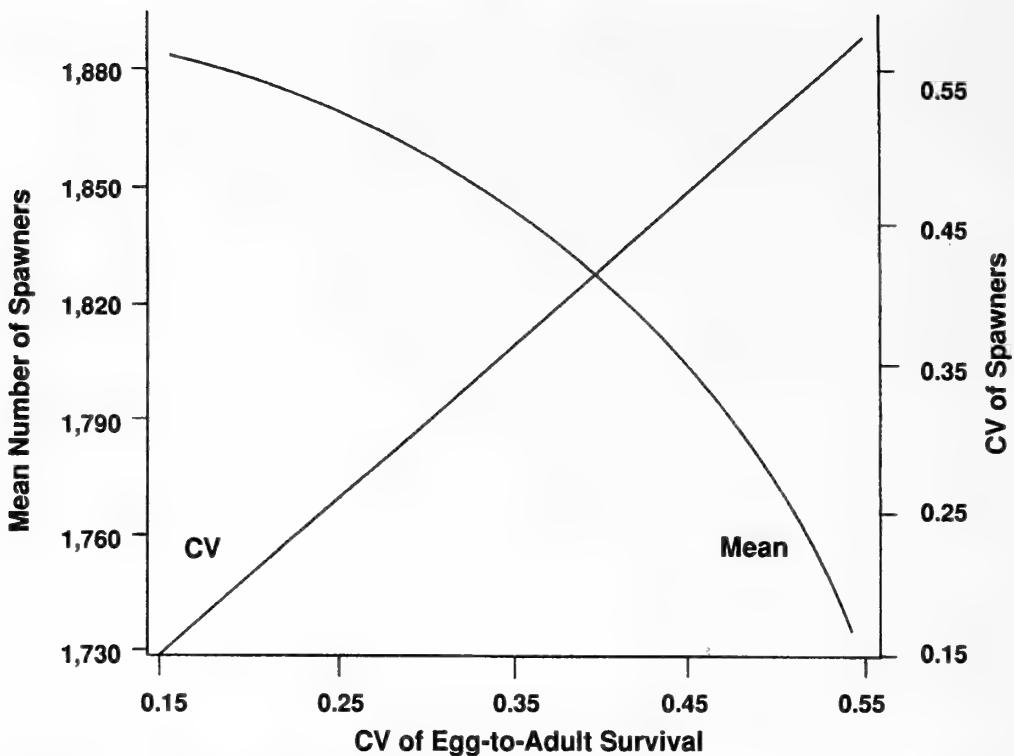
Figure 11—Effect of the coefficient of variation (CV) of egg-to-adult survival on the mean number of spawners in year 30 and the CV of spawners.

MODEL CALIBRATION

Proper calibration of a model such as the SLCM is always problematic. Rarely, if ever, is there sufficient information to provide independent estimates of all model parameters. For many stocks, the most readily available information likely will be that collected from hatchery fish, such as sex ratios and fecundity information. Given the large number of hatcheries within the Pacific Northwest, reliable information on most stocks or on stocks similar to those in question should be available. Users should be able to obtain fairly accurate estimates of the average potential egg production from a given number of spawners and estimate a variance. Howell and others (1985) and the recently completed subbasin production plans (Columbia Basin Fish and Wildlife Authority 1990) are useful sources of this type of information.

The second most readily available source of information is CWT data. The Pacific Marine Fisheries Commission maintains a comprehensive data base on tagged fish releases and recoveries for Columbia River and other Northwestern stocks. Further information on using CWT data to estimate harvest and escapement parameters is provided in appendix B. Two aspects of CWT data should be remembered: (1) most CWT data are from hatchery fish, and (2) the ratio of tags returned to the total number of tagged fish released generally is extremely small. Because most data are from hatchery fish, caution is called for when extrapolating data to naturally produced fish. Because the number of returns is so small, acute biases in parameter estimates might arise because of uneven reporting rates

from the different fisheries or recovery sites. In general, CWT data do not provide reliable estimates of the total recovery fraction (*adtrecv*) because of low, uncertain sampling rates. They likely do provide, however, the best available indication of the allocation of recovered fish among fisheries and subbasin returns.

Reliable estimates of survival parameters are very difficult to obtain. In an ideal situation, modelers would have independent data on spawner densities and smolt production, juvenile passage survival, and survival from the estuary through adulthood. Such data do not exist. For most stocks, the best available data will be in the form of a continuous record or time series of counts of individuals at a given life stage, such as estimates of the number of adults returning to the confluence of a major tributary. The trick to calibrating the model is to use these data in combination with all other sources of information to derive a set of parameter estimates that provides the best fit to the data.

A General Process for Calibration

Calibration depends in part on the version of juvenile production that is used. When using the more conventional model of juvenile survival (Version 1) is used, we found the following process to be successful. First, we obtained estimates of as many parameters as possible from the literature, opinions of experts, other models, and CWT data. From this information, we estimated all but the juvenile survival parameters and total adult recovery fraction.

Second, we estimated the general shape and magnitude of the egg-to-presmolt survival function. Direct estimates of smolt production resulting from different spawning levels generally are not available. Even if stock-recruit data are available, they usually are too scattered to allow precise estimation of a survival function. Ultimately, considerable professional judgment is needed to construct an approximate juvenile production function. The term "production function" refers to $S \cdot f(S)$, where S is the number of eggs, and $f(S)$ is the egg-to-presmolt survival function. Since the parameters of the production function and survival function are the same, the terms are interchangeable at times.

The principal factors to consider in constructing a juvenile production function are: (1) Does the function have the proper shape? (2) If the production function has a maximum, does it correspond to the level of spawning adults that would be expected to produce the maximum number of presmolts? (3) Do the relative differences in egg-to-presmolt survival at low density and at high density seem reasonable?

It is critical that the shape of the production function for juveniles be correct, since this function directly determines the compensatory capacity of the population. Accurate estimates of the absolute number of presmolts produced are less important because our principal interest is in the number of adults produced. In the final step (described below), we scale the *adtrecv* parameter so that the combined parameter set provides the best fit to the available data, and compensates for some of the error we might have introduced through estimates of other parameters.

The final step in calibration is to estimate *adtrecv, cvegsv,* and *cvadtrv.* For this purpose, a second ancillary model has been constructed. The calibration model uses the parameters of the SLCM and deterministic analogs of its relationships to predict elements of a historic time series using previous observations in the time series. The parameter *adtrecv* is introduced

as a vector of annual coefficients that is adjusted systematically to minimize the sum of squared errors between observed and predicted observations. Users can set constraints on the annual coefficients so that they fall within a given range. The mean of the fitted vector is then used as an estimate of *adtrecv*.

The calibration model also calculates the mean and variance of the product of egg-to-presmolt, downstream migrant, and smolt-to-adult survival for each cohort. The variance of this product is partitioned among the three survival components algebraically. Since there is only one variance equation but three unknowns, the user must decide the relative proportions of the variance to be allocated to each life stage, or alternatively must set one or two of the component variances to a constant and solve for the remainder.

Calibration Using the Alternative Model of Juvenile Production

The calibration process for the alternative model of juvenile production (Version 2) is similar in concept to that described above. Smolt-to-adult survival again is used as a scaling factor to provide the best fit to the data. Paulsen and others (1991) provide an example using this version of the model.

CONCLUSIONS

The SLCM has proven to be a powerful and flexible tool for examining the impact of changes in population parameters on the structure and size of salmonid populations. While some aspects of the SLCM's behavior have been difficult to understand at first glance, the model's overall behavior conforms well to theory and experience with deterministic models. Some of the more provocative results are those that deviate from an analogous deterministic model, such as the model's sensitivity to parameter variance. As our experience with the model grows, we expect new questions to arise concerning the interplay of stochastic factors and population dynamics, opening new areas of research. Such questions, and their answers, could have significant management implications.

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APPENDIX A—A PROCESS FOR ADJUSTING EGG-TO-PRESMOLT SURVIVAL WHEN HATCHERY FISH ARE INTRODUCED

I. Definitions

p1 = probability of survival of naturally produced eggs with no additional hatchery fish

p2 = p1 adjusted for presence of hatchery fish

p3 = p2 adjusted for time period

$N(t)$ = natural fry alive at time t

$H(t)$ = hatchery fry alive at time t

μ1 = instantaneous mortality rate

μ2 = adjusted mortality rate

E($\bullet$) = denotes expectation

Binomial{N,p} = function call that generates a random number from a binomial distribution.

Beta{p,cv} = function that generates a random number from a beta distribution

f{x} = function call to density-dependent relationship that defines p as a function of x

All other definitions are as defined within the text.

II. Calculations

Calculations take place in sequence

1. μ1 = –log(p1)/100
2. N(*reltime*) = Binomial{EGGS,exp(–μ1*reltime)
3. H(*reltime*) = Binomial{*hatfry,hintsv*
4. E(p2) = f{EGGS+H(*reltime*)}
5. μ2 = –log(p2)/100
6. E(p3) = exp(–μ2*(100–*reltime*))
7. p3 = Beta{E(p3),*cvegsv*}
8. PRESMOLT = Binomial{N(*reltime*)+H(*reltime*),p3}

APPENDIX B—AN EXAMPLE OF HOW TO ESTIMATE OCEAN AND IN-RIVER PARAMETERS FROM CWT DATA

Snake River Fall Chinook CWT Data

Number released: release = 1,467,443

Recoveries:

Ocean harvest	In-river harvest	Hatchery returns
o1 = 2,105	r1 = 1,390	h1 = 1,078
o2 = 12,608	r2 = 4,716	h2 = 188
o3 = 2,137	r3 = 1,938	h3 = 142
o4 = 92	r4 = 121	h4 = 4

Assumption

Survival from release site to below Bonneville dam: surv = 0.3

Calculations

$$\text{total} = o1 + o2 + o3 + o4 + r1 + r2 + r3 + r4 + h1 + h2 + h3 + h4$$
$$\text{sum1} = \text{total} - (o1 + r1 + h1)$$
$$\text{sum2} = \text{sum1} - (o2 + r2 + h2)$$
$$\text{sum3} = \text{sum2} - (o3 + r3 + h3)$$

adtrecv = total / (release • surv)	adtrecv = 0.06
ocn1hav = o1 / total	ocn1hav = 0.079
ocn1suv = sum1 / total	ocn1suv = 0.828
ocn1rvh = r1 / total	ocn1rvh = 0.052
ocn1sbe = h1 / total	ocn1sbe = 0.041
ocn2hav = o2 / sum1	ocn2hav = 0.575
ocn2suv = sum2 / sum1	ocn2suv = 0.202
ocn2rvh = r2 / sum1	ocn2rvh = 0.215
ocn2sbe = h2 / sum1	ocn2sbe = 0.009
ocn3hav = o3 / sum2	ocn3hav = 0.482
ocn3suv = sum3 / sum2	ocn3suv = 0.049
ocn3rvh = r3 / sum2	ocn3rvh = 0.437
ocn3sbe = h3 / sum2	ocn3sbe = 0.032
ocn4hav = o4 / sum3	ocn4hav = 0.424
ocn4rvh = r4 / sum3	ocn4rvh = 0.558
ocn4sbe = h4 / sum3	ocn4sbe = 0.018

APPENDIX C—EXAMPLE CONTROL FILE AND PARAMETER INPUT FILES

C.1 Control File

```
*********************************************************************************
*      CONTROL FILE FOR RUNNING THE STOCHASTIC LIFE CYCLE MODEL               *
*********************************************************************************
*    CHANGES IN THIS FILE SHOULD BE MADE ONLY TO LOWER CASE IDENTIFIERS.      *
*           DO NOT DELETE ANY SEMICOLONS OR OTHER SPECIAL CHARACTERS!!!       *


*********************************************************************************;

%INCLUDE 'macro6_1.sas' /source2;
***********************************************
*   PART 1.  CONTROL MACRO AND KEY FILES      *
***********************************************;
LIBNAME SASLIB 'slcmout';            /* DIRECTORY FOR SAS OUTPUT FILES */
FILENAME J_PARMS 'test61j.par';      /* FILE WITH PRODUCTION PARAMETERS */
FILENAME P_PARMS 'testp.par';        /* PASSAGE PARAMETERS FOR WILD SMOLTS*/
FILENAME HP_PARM 'testp.par';        /* PASSAGE PARAMETERS FOR HATCHERY SMOLTS*/
FILENAME A_PARMS 'testa.par';        /* FILE WITH ADULT PARAMETERS (WILD) */
FILENAME HA_PARM 'testa.par';        /* FILE WITH ADULT PARAMETERS (HATCHERY) */
FILENAME INITIAL 'initnum.exp';      /* FILE WITH INITIAL NO. (WILD HAT.) */
%LET RESULTS = expl61 ;              /* SAS DATASET TO CONTAIN MODEL OUTPUT   */
%LET JUVPARM = facbase ;             /* HANDLE FOR ACCESSING PRODUCTION PARAMETERS */
%LET PASS = %STR('test1') ;          /* HANDLE FOR PASSAGE PARAMETERS */
%LET ADULT = %STR('test1') ;
     /* HANDLE FOR ADULT RECOVERIES */
%LET HATCHERY = %STR('on') ;         /* TURNS HATCHERY PRODUCTION ON OR OFF */

%MACRO CONTROL;
          NGAMES  = 500;             /* NUMBER OF GAMES  */
          YEARS   = 50;              /* NUMBER OF YEARS PER GAME */
          SMTTOG  = 1;               /* SPECIFY SMOLT PRODUCTION OPTION */
%MEND CONTROL;
***********************************************************
*   PART 2.  IDENTIFY STEPPED VARIABLE AND LEVELS         *
***********************************************************;
%LET STEPVAR = noparm;               /* DEFINE STEPPED VARIABLE */
%MACRO STEPDEF;
          NSTEPS = 1  ;              /* DEFINE NUMBER OF STEPS, 1 OR MORE   */
          LEVEL1 = 1  ;              /* DEFINE VALUES FOR EACH STEP.         */
          LEVEL2 = 0  ;              /*   UP TO TEN LEVELS ARE PERMISSIBLE  */
          LEVEL3 = 0  ;
          LEVEL4 = 0  ;
          LEVEL5 = 0  ;
          LEVEL6 = 0  ;
          LEVEL7 = 0  ;
          LEVEL8 = 0  ;
          LEVEL9 = 0  ;
          LEVEL10 = 0  ;
%MEND STEPDEF;
```

```
**************************************************************
*   PART 3.   IDENTIFY YEAR-DEPENDENT PARAMETERS AND VALUES  *
*        FOR VARIABLES OTHER THAN PASSAGE AND OCEAN HARVEST  *
**************************************************************;
%MACRO VARYEAR;   /* OPTIONAL SUBROUTINE */
 *SELECT;
          *WHEN (0 < YEAR <= 2) DO;
                *parm = value;
          *END;
            *WHEN (2 < YEAR <= 5) DO;
                  *parm = value
             *END;
             * et cetera;
             *OTHERWISE parm = value;
 *END;
 %MEND VARYEAR;


*********************************************************
*   PART 4.   IDENTIFY OUTPUT VARIABLES OF INTEREST     *
*********************************************************;
%MACRO KEEPLIST;   /* THESE VARIABLES WILL BE INCLUDED IN OUTPUT FILE */
    KEEP STEP &STEPVAR STOCK GAME YEAR STRATID P_OPTION H_OPTION
          subesp subharv recruits spawners hsubesp hsubharv hrecruit hspawn
          espwild;
    stratid = 'test case';      /*  IDENTIFY STRATEGY */
    P_OPTION = &PASS;
    H_OPTION = &ADULT;
%MEND KEEPLIST;


*********************************************************
*   PART 5.   OUTPUT CONTROL                           *
*********************************************************;
%MACRO YEAROUT;
          ALLYEARS= 'Y'     ;       /*  PUT Y IF OUTPUT WANTED EACH YEAR,  */
                                    /*  PUT N IF OUTPUT ONLY ON LAST YEAR  */
%MEND YEAROUT;


*********************************************************
*   PART 6.   CALLS TO OTHER PROGRAMS                  *
*********************************************************;
%INCLUDE 'slcm6_1.mod' /SOURCE2;
```

C.2 Production Parameters

```
*** filename: test61j.par ;
FACBASE:     /* Identifies a specific parameter set */

***  Natural Production Parameters ***;
stock =            3;       /* stock identifier */
ffem =         0.583;       /* fraction female  */
prspsv =        0.85;       /* prespawning survival */
egfem =         4297;       /* mean eggs per female */
stdegg =         233;       /* std. error of egfem  */
jackspn =          0;       /* spawning contribution of 1-ocean fish */
logtscl =        1.0;       /* logit scale parameter  */
alpha =        -1.73;       /*  density-indp. juvenile survival parm.  */
beta =     -8.41e-08;       /* density-dep. juvenile survival parm.  */
```

```
cvegsv =           0.2;       /* CV of egg-to-presmolt survival */
stay1 =            0.15;      /* cond. prob. of staying over 1st winter */
stay2 =            0;         /* cond. prob. of staying over 2nd winter */
stay3 =            0;         /* cond. prob. of staying over 3rd winter */
inbsmsv =          0.5;       /* inbasin overwinter survival  */
basercv =          0.15;      /* fraction recovered as adults */
cvadtrv =          0.3;       /* CV of basercv */
minesp =           600;       /* minimum escapement goal */
maxthar =          100;       /* maximum terminal harvest */

***  Hatchery Stock Parameters  ***;
hffem =            0.583;     /* fraction female  */
hprspsv =          0.85;      /* prespawning survival */
hegfem =           4297;      /* mean eggs per female */
hstdegg =          233;       /* std. error of egfem  */
egg_fry =          0.8;       /* egg-to-fry survival rate */
hfry_sv =          0.6;       /* initial subyearling surv. following release */
fry_smt =          0.8;       /* fry-to-smolt survival rate */
hsmt_sv =          0.7;       /* initial yearling surv. folowing release */
hjackspn =         0;         /* spawning contribution of 1-ocean fish */
hbasercv =         0.1;       /* fraction recovered as adults */
hcvadtrv =         0.3;       /* CV of basercv */
hstray =           0.5;       /* conditional contribution to wild escapement */
htermhar =         0.9;       /* terminal harvest rate  */

*** Hatchery Management Parameters ***;
adtsup =           0;         /* additional adult supplementation to wild */
colrate =          0.1;       /* hatchery collection efficency of wild fish */
hcolrate =         0.8;       /* collection efficiency of hatchery fish */
minrun =           500;       /* minimum wild subesp before hatchery take */
hatrem =           20;        /* target take by hatchery of wild adults */
hatneed =          200;       /* total number of adults needed by hatchery */
htarget =          0.3;       /* minimum acceptable frac. of hat. egg capacity */
eggcap =        500000;       /* hatchery egg capacity */
fryplant =         0.05;      /* fraction of hat. fry released as subyearlings */
fryint =           10;        /* level of interaction between natural and
                                 supplemented hatchery subyearlings (0 - 100) */
RETURN;
```

C.3 Passage Parameter File

filename: testp.par

JUVENILE PASSAGE TEMPLATE

The basic format for this data set is to place an asterisk in the first
column of the line containing the scenario identifier followed by a
variable which indicates how many lines of data follow that are
specific to that scenario. Data lines consist of three variables:
msurv (mean survival), passcv (CV of passage survival), and
nyr (the number of years for which the passage parameters apply).

```
              msurv        passcv       nyr
    * base 5
              0.24         0.2            1
              0.26         0.21           2
              0.27         0.15           2
              0.3          0.3            4
              0.32         0.31           2

    * test1 5
              0.24         0.2            1
              0.27         0.23           2
              0.3          0.25           3
              0.32         0.33           4
              0.35         0.4            2
```

C.4 Adult Recovery File

filename: testa.par

ADULT RECOVERY PROFILES TEMPLATE (CONTRIVED EXAMPLE)

The basic format places an * in the first column of the row containing
the scenario identifer, followed by the scenario id and nk, a parameter
which tells how many years of data follow. The first year of data MUST
be data representing the calibration years. The general format for the
data lines is as follows:

```
        begin   - escapement —  ocean harvest    river harvest
    year number  e1   e2   e3  e4  o1   o2   o3  o4  r1   r2   r3  r4

* base 5
    1989   1600  19  201  82  10  35  453  355  36  46  172  248  44
    1990   1000   8   88  35   5  16  198  157  16  21   76  109  19
    1991   2800  25  273 112  14  49  614  483  48  62  235  339  61
    1992   1800  16  174  72   9  32  389  304  30  40  150  218  39
    1993   1200   7   77  32   4  14  171  133  13  17   67   97  17

* test1 5
    1989   1600  19  201  82  10  35  453  355  36  46  172  248  44
    1990   1000  11   99  36   5  16  204  156  16  12   47  108  19
    1991   2800  38  290 119  15  52  651  512  51  42  250  360  65
    1992   1800  18  190  79  10  33  428  331  34  44  163  238  43
    1993   1200   8   90  37   5  16  199  157  15  21   77  113  20
```

A stochastic model simulating the life cycle of anadromous salmonids that mimics the basic mechanisms regulating populations of Pacific salmon is presented. The SLCM incorporates stochastic or probabilistic processes at each step in the life cycle. The model's predictions are expressed in probabilistic terms. The model is designed to use inputs from more detailed models for specific life stages, in combination with a minimum number of empirically based parameters. Users can choose among three density-dependent relationships to describe egg-to-smolt survival and among a variety of scenarios involving hatchery and natural production, ranging from natural production only, to production supplemented with hatchery adults or juveniles. The model is written in the SAS® programming language, which allows it to be used on a variety of computing systems and enhances flexibility in analyzing model output.

INTERMOUNTAIN RESEARCH STATION
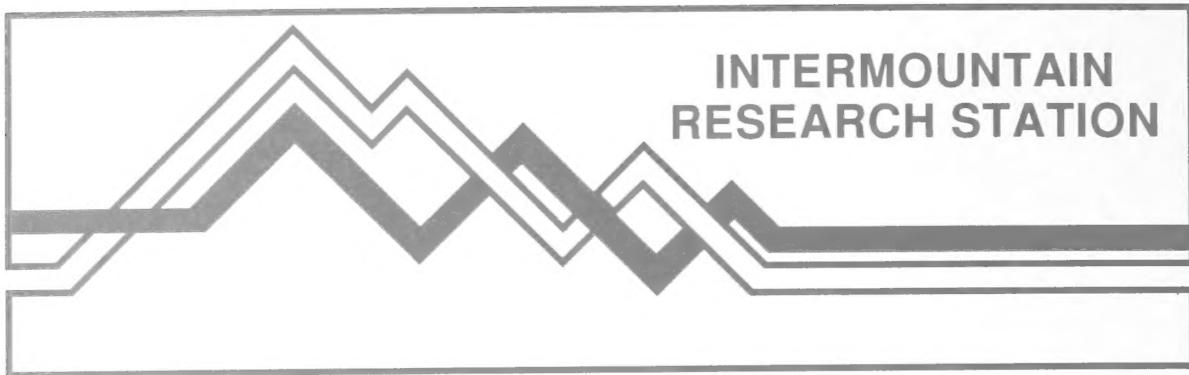
The Intermountain Research Station provides scientific knowledge and technology to improve management, protection, and use of the forests and rangelands of the Intermountain West. Research is designed to meet the needs of National Forest managers, Federal and State agencies, industry, academic institutions, public and private organizations, and individuals. Results of research are made available through publications, symposia, workshops, training sessions, and personal contacts.

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